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Coastal Vegetation

Second Edition

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COASTAL VEGETATION

SECOND EDITION

by

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PREFACE TO FIRST EDITION

THIS book is one of a series designed to give a general account of the ecology of types of British vegetation. Coastal vegetation differs greatly in various parts of the world and an author can be faced with the problem of how far afield he should wander. Bearing in mind the purpose of this volume, the text has been restricted almost wholly to the ecology of British vegetation. This has not proved difficult in the descriptive sections, but when dealing with the factors of the habitat it might be thought more reference should have been made to studies outside of Great Britain. This could have involved different climatic regions and the inevitable occasional reference to vegetation unfamiliar to residents of Great Britain, and so it has been omitted. Because it is hoped that one result of this book will be to encourage Sixth Formers and First Year undergraduates to read accounts of the local vegetation whenever it is available, every effort has been made to include at the end of each chapter all known references to specific works on that particular aspect of British coastal vegetation, whether it is referred to in the text or not.

No book of this nature could be prepared without advice and critical comment from those who have particularly worked on coastal areas. I wish, therefore, to express my sincere thanks to Professor J. A. Steers for comments on the salt marsh and shingle beach chapters, to Dr D. S. Ranwell for criticism of the salt marsh and sand dune chapters, to Dr M. Gillham for helpful advice on the coastal cliff chapter, and to Mr D. J. Chapman for comments on the chapters dealing with the littoral. I am also most grateful to my colleague, Professor J. E. Morton, for reading the whole manuscript and for valuable discussions with him on problems of the littoral. Finally, there is my deep appreciation of the advice and help given me by the series editor, Professor G. F. Asprey, and Dr A. G. Lyon of his staff. Their comments and help have undoubtedly improved the final product, though I must remain responsible for opinions expressed and the general accuracy of statements.

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Auckland V. J. CHAPMAN

PREFACE TO SECOND EDITION

THIS new edition has been enlarged in order to include comparable types of coastal vegetation on the eastern shores of the U.S.A. as well as vegetation of the northern European Atlantic shores. Recent work in all fields of coastal vegetation has been drawn upon in compiling this new edition and the bibliography has been considerably extended. This new edition no longer deals exclusively with British coastal vegetation but with the coastal vegetation of the North Atlantic. It is hoped that this new edition will be of use to University students in Great Britain, northern Europe and the eastern U.S.A.

Auckland V. J. CHAPMAN

CHAPTER 1

BASIC ECOLOGICAL PRINCIPLES

In this book coastal vegetation will be regarded as comprising (a) the marine algal vegetation of the littoral and sublittoral, (b) the phanerogamic and algal vegetation of salt and brackish marshes, (c) the vegetation of sand dunes together with that of their "slacks", (d) the specialised vegetation associated with the drift-line, (e) the vegetation of shingle beaches, (f) the plants found on coastal cliffs and (g) mangrove (Florida).

These habitats are specialised and well defined so that they readily lend themselves to ecological study. Furthermore, such environments possess specific features that are reflected in the type of plants found growing there, so that they are of especial interest. Moreover, within at least five of these habitats one can find excellent examples of the phenomenon of vegetation *zonation*. Such zonation is invariably associated with a gradation in one or more of the environmental factors, and one of the major functions of any ecological study is to establish those factors responsible for any zonation that can be observed.

ZONATION

When any particular habitat has been selected for study, the first procedure is to become familiar with, and identify, all the plants that can be found. The next step is to determine the exact nature of any zonation that can be observed and to list the various species that are apparently typical of each zone or belt. A consideration of the habitat should then indicate whether the zoning is permanent (static) or whether it is in a state of flux (dynamic). Thus zoning of the vegetation of the littoral, of shingle beaches and less obviously, often possibly non-existent, of coastal cliffs, will be of a static nature, not changing unless there is a variation in land-sea-level relationships or a large scale change induced by a major cliff-fall or slump. The zoning of the vegetation of salt marshes, mangroves and sand dunes will be dynamic or developmental, so that in any one spot on a salt marsh or mangrove swamp, as more mud is deposited and the land level rises with consequent environmental changes, the flora also gradually changes. A similar story can likewise be observed on sand dunes as successive ridges form on the shore, the oldest dunes with the most mature vegetation being to the landward, while the youngest dunes with relatively few species and incompletely colonised are to the seaward.

The communities associated with static zonation represent what some schools of ecology term *climax* communities. There are those who believe that only one kind of climax, the climatic climax, is represented in any one area. There are others who consider that there may be more than one kind of climax in an area. In the case of the littoral and of shingle beaches it can be argued that the physiography determines the zonation, and therefore the communities represent a physiographic climax. Whilst the idea of climax vegetation, or vegetation in equilibrium with the environment, may commend itself to many, there are those who argue that there is no such thing as a climax. Until one has had an opportunity of studying and comparing many stands of vegetation from comparable habitats, it is premature to discuss the validity or otherwise of the climax concept. In the meantime, however, it is convenient for us to accept the climax as a useful concept.

SUCCESSION

Developmental or dynamic zonation is more commonly called plant succession, because starting from bare ground one can observe a series of communities that succeed one another until the final or climax community is attained. When the succession commences on bare ground not previously colonised it is known as a *prisere*. The successions that are to be observed on sand dunes, salt marshes and mangrove swamps are good examples of priseres (see Chapters 4, 6 and 8). Should an area of dune that has developed to forest become destroyed by burning a new succession would arise, but this would be known as a *subsere*.

Subseres in coastal habitats are of rare occurrence, and the student can generally be assured that he is dealing with a prisere. Under certain conditions the succession may be halted, or it may revert to a previous stage or it may deviate through another series of communities. The advent of a dense population of browsing animals can result in the next stage of the succession not developing. Thus it is probable that excessive grazing of some of the west coast grass marshes (see p. 108) and former hay cutting of marsh grass on Atlantic East Coast marshes has delayed or prevented the advent of the rush or *Juncus* stage. Excessive grazing on salt marsh may damage the soil surface to such an extent that the closed herb cover disappears and is replaced by annual *Salicornia* (Saltwort) or *Suaeda* (Seablite), both generally representative of an earlier stage. Over-grazing of coastal cliffs brings about replacement of Creeping fescue (*Festuca rubra*) by Sea pink (*Armeria maritima*) or Sea plantain (*Plantago maritima*) (see p. 257). Deviation of a succession is not common with coastal vegetation, but it has been recorded on Nova Scotian salt marshes where it was produced as a result of persistent mowing for hay grass.

Sand dunes, especially their damp valleys ("slacks"), can provide examples of another ecological phenomenon, namely, *cyclic change*. This is sometimes known as pattern and process. In this there is a build-up to a vegetation covering which then becomes destroyed, either as a result of smothering by lichens or mosses or through damage from animals or man, resulting ultimately in the complete removal of the vegetation with a new bare surface on which the succession starts afresh (see p. 176). This process differs from a halted or deflected succession in that there is a regular continuing sequence, whereas in the others the induced stages only exist so long as the factor, e.g. grazing, cutting, persists.

During the normal course of a succession, the early stages can be regarded as far removed from equilibrium with the environment or habitat, successive communities becoming more and more in harmony with it, so that when the climax state is attained the final community is in equilibrium with the habitat. During the course of a succession, each successive community adds to what may be called the habitat potential, or the degree to which the habitat is increasingly capable of accepting a new and perhaps wider range of plant species. This concept is illustrated schematically in Fig. 1.1, where it will be noted that each community of the succession is marked by a pioneer or invasion stage (P), a Building stage (B), and a mature (M) stage which is eventually invaded by the pioneers of the next community.

Because the study of salt marshes, mangroves and sand dunes involves the study of successions, it is perhaps worth while to make brief reference to what may be called the nature of the succession.

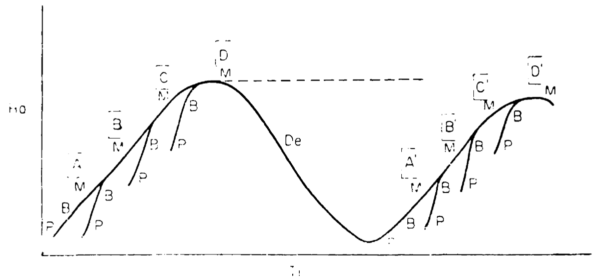

FIG 1.1. *Build-up through successive communities to a climax. Each community passes through a pioneer* (P), *building* (B) *and mature* (M) *phase. This development is plotted in terms of build-up of habitat potential* (Ha) *with time* (Ti). *When degradation* (De) *takes place the process is repeated (after Chapman).*

The first stage is the existence of the bare ground which arises as deposited mud in the case of salt marshes and mangroves or as blown sand in the case of dunes. The bare ground then becomes invaded by the first colonists. Invasion depends on a variety of factors and again it is the function of the ecologist to try and determine these factors and analyse their importance. Such factors include proximity of potential seed parents, method of seed dispersal (i.e. wind, animals or sea) or whether by vegetation fragments (as may be the case with *Spartina townsendii*, see p. 145) when the direction and strength of long-shore currents must be very important.

The arrival of the seeds is followed by the next stage, which is often called *ecesis*. This involves the successful germination of the seed (and the existence, therefore, of suitable temperatures and water supply and the absence of predators), successful growth of the plant to maturity (determined and controlled by the factors of the environment or habitat), flowering and the setting of seed so that the community is perpetuated.

The advent of the plants brings about changes in the habitat. Thus organic matter from dead plants is added to the soil, in the case of salt marshes and sand dunes the presence of the plants results in the former case in increased silt deposition, and in the second case in fixation of the sand so that it is no longer so mobile. The plants also bring about changes in the soil nutrients and soil water supply, and these changes may be further reflected in the soil microflora and fauna (see p. 208). If the plants happen to be of some size, they will also bring about changes in the micro-climate, e.g. air movement, surface evaporation and relative humidity, and these changes may determine the nature of other species that subsequently invade the community. All these changes and effects upon the habitat can collectively be termed *reaction*.

Invasion and reaction result in more plants entering the former area, and usually at quite an early stage *competition* for soil nutrients, soil water and even light may become important features of the community. This competition is likely to reach its maximum for any species just around the period of flowering, when plants generally make their greatest demand on the habitat. A community could therefore be regarded as more successful if the flowering periods of its principal species do not all occur at the same time.

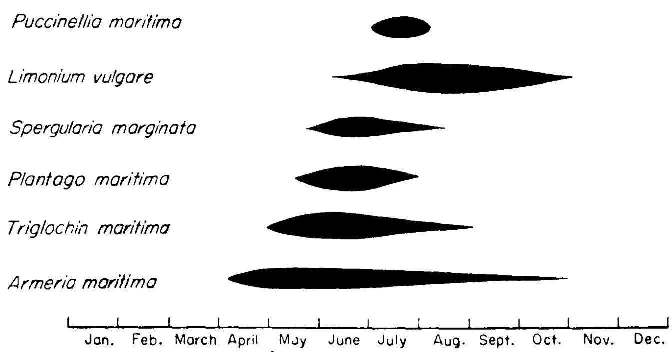

FIG. 1.2. *The flowering periods of the six species comprising the General Salt Marsh community at Scolt Head (after Chapman).*

In the case of the General Salt Marsh community (see p. 108) where there are a number of co-dominant species, the flowering times are staggered (Fig. 1.2). This is one aspect of coastal ecology that merits much more attention, not only in respect of actual flowering periods, but in determining the demands made by the principal species at different stages of their life history.
The final stage in the succession is *stabilisation*, when the climax community is reached, and with it comes dominance of the principal life-form. Earlier stages will have exhibited the phenomenon of dominance of one or more species as such, but in the climax community one has not only dominance of species but also of a particular life-form (see p. 8), which under normal, non-extreme climatic conditions is generally trees.

COMMUNITY ANALYSIS

Whether one is dealing with a static zonation, and hence climax communities, or a developmental zonation (succession), it is important to be able to describe the communities in such a way that they can be compared with similar communities elsewhere. One also needs to know the extent of variation within any given community.

One way of doing this after recognition of the community, which is generally possible by eye, is to prepare a list of the species, including if at all possible the animals. However, a species list is not of itself sufficient. We must know something of the relative frequency or abundance. This has been done by making use of terms such as dominant, abundant, frequent, occasional, rare, local, etc., but it is evident that such terms are subject to individual interpretation. Analysis of the community is therefore much more satisfactory if this kind of interpretation can be eliminated.

Some communities are very large, and whilst it may be easy to prepare a species list, detailed analysis of the entire community would take far too long. Use is made instead of samples, these being commonly contained within a square area known as a quadrat. The size of the quadrat must be such that it yields a fair statistical sample of the community. There are various ways of determining the minimal area that will give a fair sample of a particular type of community, and for those interested reference should be made to standard ecological texts (2,9,10). Generally speaking, on sand dunes, shingle beaches and salt marshes, one square metre is likely to be sufficient, and at least ten such quadrats should be used for each community. On the rocky sea coast smaller areas may be adequate for the seaweed vegetation. In the case of a mangrove swamp quadrats should be at least a hundred square metres, but a ten metre wide belt transect from sea front to upland is almost better. Traditionally the quadrat is a square, but under certain conditions a rectangle with sides in the ratio 1 : 16 may be better, or a belt transect of one or two metres wide can be employed. In the succeeding chapters reference will be made to investigations that have involved use of all these variants.

With low vegetation it is also possible to make use of what is known as the "point method" where a long pin is repeatedly stuck in the ground and the species physically touched are listed. For the use of this technique, reference should be made to works by Goodall(8)and Greig-Smith (9). With quadrats, which should normally be located at random, one can provide lists of species occurring, numbers of individuals of species, or one can map the quadrat showing the species spatially distributed. So long as the quadrats are all located in the same community, one can determine what is known as frequency, density, abundance and percentage cover:

$$\text{frequency} = \frac{\text{No. of occupied quadrats}}{\text{Total no. of quadrats}} \times 100$$

$$\text{density} = \frac{\text{Total no. of individual plants}}{\text{Total no. of quadrats}}$$

$$\text{abundance} = \frac{\text{Total no. of individual plants}}{\text{No. of occupied quadrats}} \times 100 \quad \frac{\text{density}}{\text{frequency}}$$

Cover percentage = percentage of ground covered in the quadrats by a perpendicular projection of the aerial parts of the individual plants on to the quadrat.

This is not the place to enter into a discussion of the relative value and significance of the figures for frequency, abundance, density and cover, but before any of them are used, reference should be made to Greig-Smith (9).

Biological material is notoriously variable and any field method is also subject to experimental error. The increasing application of mathematical methods in ecology is designed to overcome these problems. Presentation of the results of mathematical analysis in the form of histogram and scatter diagrams etc. is also desirable. Most mathematical ecological analyses involve the use of variance, standard error, linear regression, t test and χ^2 test for association and the use of probability tables. All these techniques will be found in the relevant text books (2,10).

Use can be made of some of the data in order to arrive at what is often known as a *coefficient of similarity* or *coefficient of community*, whereby two different or two apparently similar communities can be compared. There are various ways of arriving at such coefficients, and those interested should